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Larval Development in the Lutjanid Subfamily Lutjaninae (Pisces): the Genus *Macolor*

JEFFREY M. LEIS

Ichthyology, Australian Museum, 6 College Street, Sydney NSW 2010, Australia
jeff.leis@austmus.gov.au

ABSTRACT. Larval development of the Indo-west Pacific lutjanine lutjanid *Macolor niger* is described based on pelagic larvae (4.8–10 mm) from western Pacific plankton hauls, settlement-stage larvae (17–19 mm) from Great Barrier Reef light-trap catches and Solomon Island reef-crest net catches, and settled juveniles (26–32 mm) from the western Pacific. The larvae possess all the characteristics of lutjanids (24 myomeres; elongate dorsal spine 2 and pelvic spine; pelvic ray 1 longer than spine; postcleithral spine; extensive, large, smooth head spines; and fin-ray counts of DX,14–15, AIII,10–11, P_1 17–18), and corroborate the inclusion of *Macolor* in the Lutjanidae. The larvae have long, weakly serrate, robust fin spines, with the serrations largely disappearing by settlement at 17–19 mm. Unique meristic values (in particular fin-ray and gill-raker counts) and distinctive colour pattern at settlement confirm the identification. Settled juvenile *M. macularis* (17–20 mm) from the western Pacific are similar to *M. niger*, but are slightly deeper bodied, with much longer elements in the pelvic fin and spiny dorsal fin. Distinctive meristics and pigment patterns separate the two species.

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The perciform fish family Lutjanidae, or tropical snappers, consists of about 125 species of medium to large fishes of great ecological and commercial importance arrayed in five subfamilies (Johnson, 1993; Nelson, 1994). The largest lutjanid subfamily, Lutjaninae, (sensu Johnson, 1980) contains six genera: *Hoplopagrus* (east Pacific, monotypic), *Lutjanus* (worldwide, c. 70 species), *Macolor* (Indo-west-Pacific, two species), *Ocyurus* (west Atlantic, monotypic), *Pinjalo* (Indo-west-Pacific, two species) and *Rhomboplites* (west Atlantic, monotypic). Descriptions of larvae of at least some species in most lutjanine genera have been published or are in preparation. Larvae of several *Lutjanus* species have been described (see summaries in Kojima, 1988; Watson & Brogan, 1996; Leis & Rennis, 2004; Lindeman *et al.*, 2005), and descriptions of seven more Indo-Pacific *Lutjanus* species are in preparation (JM Leis, unpublished). Larvae of the monotypic genera *Hoplopagrus, Ocyurus* and *Rhomboplites* have been described (summarized in Watson & Brogan, 1996; Lindeman *et al.*, 2005), and a description of the larvae of both *Pinjalo* species is in preparation (JM Leis, unpublished). Larvae of *Macolor*, in contrast, have not been described.

The two species of *Macolor* Bleeker—*M. niger* (Forsskål) and *M. macularis* Fowler—are closely associated with coral reefs and are widely distributed in the western Pacific and Indian Oceans (Kishimoto *et al.*, 1987). Once confusion over its marked ontogenetic changes was resolved, *M. niger* was long considered the sole *Macolor* species, and although originally placed in the sciaenid genus *Sciaena* by Forsskål, and occasionally considered a serranid (Günther, 1873) it has been placed in the Lutjanidae by consensus since at least the end of the nineteenth century. Several workers placed

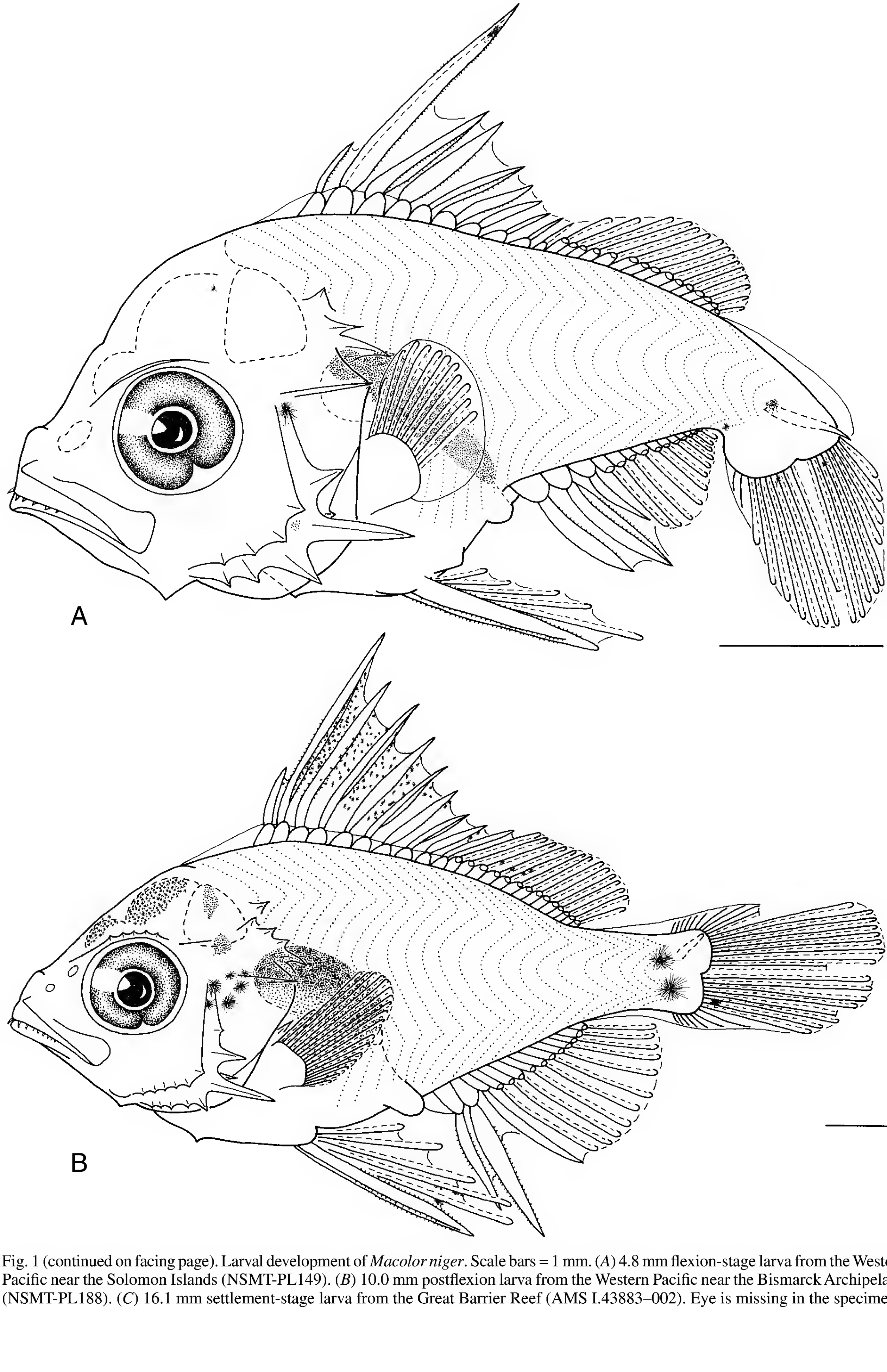

Fig. 1 (continued on facing page). Larval development of *Macolor niger*. Scale bars = 1 mm. (*A*) 4.8 mm flexion-stage larva from the Western Pacific near the Solomon Islands (NSMT-PL149). (*B*) 10.0 mm postflexion larva from the Western Pacific near the Bismarck Archipelago (NSMT-PL188). (*C*) 16.1 mm settlement-stage larva from the Great Barrier Reef (AMS I.43883–002). Eye is missing in the specimen.

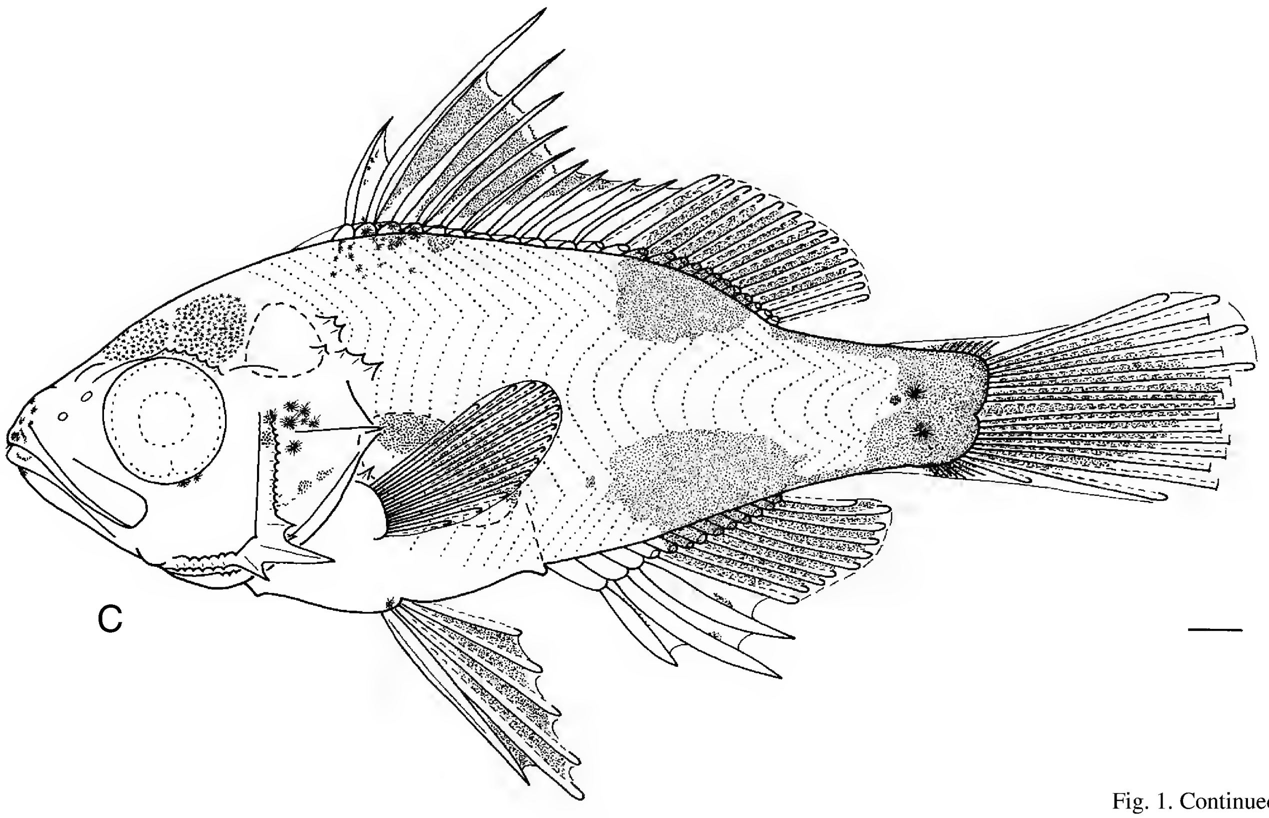

Fig. 1. Continued.

M. niger in the genus *Lutjanus* or its synonyms *Genyroge* or *Mesoprion* (Günther, 1859; Bleeker, 1876; Fowler, 1928, Weber & de Beaufort, 1936), but *Macolor* has been recognized by nearly all workers as a valid genus since the middle of the twentieth century (Schultz, 1953). Kishimoto *et al.* (1987) revised *Macolor* and showed that there are, in fact, two species, both of which undergo marked ontogenetic changes in body shape and colour.

Adult *Macolor* spp reach sizes of over 400 mm SL and are dark-coloured with deep bodies and rounded snouts. They occur singly and in small groups (*M. macularis*) or form large schools (*M. niger*) feeding on zooplankton in high current areas, usually off steep underwater slopes, dropoffs or cliffs, where they can be very abundant (Randall *et al.*, 1997; Myers, 1999; Randall, 2005). Juveniles differ greatly in appearance from adults: they have a contrasting black and white colour pattern that begins to transform to the adult colour pattern at about 200 mm SL (Kishimoto *et al.*, 1987; Randall, 2005). Juveniles live in lagoonal and reef-front habitats where, unlike the adults, they are solitary (Myers, 1999, pers. obs.).

Recently-settled juveniles are distinctively pigmented, and have elongate dorsal-fin spines and pelvic-fin rays, especially *M. macularis* (Kishimoto *et al.*, 1987). The dorsal fin is notched and the black pigment pattern accentuates this, providing, at first glance, a resemblance to some apogonid species (pers. obs.) or to juveniles of some species in the haemulid genus *Plectorhinchus* (Myers, 1999). In spite of the abundance of adult *Macolor* species on coral reefs, larvae are extremely rare in collections. Over the course of some years, I have searched the major larval-fish collections of the world for lutjanid larvae, and have found only a few *Macolor* larvae.

My purpose here is to describe the larval development of *M. niger* based on two pelagic larvae captured by the Japanese research vessel "Shunyo Maru" in the western Pacific, and four settlement-stage larvae captured by light trap on the Great Barrier Reef and crest net in the Solomon Islands. I also provide information on two recently-settled *M. niger* from the Ryukyu Islands and Samoa. Finally, although no larvae of *M. macularis* are available, I describe aspects of three recently settled *M. macularis* from the Ryukyu Islands that may assist in identification of larvae of this species. Larval development in other lutjanid subfamilies is described in the following: Etelinae (Leis & Lee, 1994; Leis, 2005), Apsilinae (Leis *et al.*, 1997), Paradicichthyinae (Leis & Bray, 1995), and Caesioninae (Reader & Leis, 1996).

Materials and methods

Measurements and abbreviations follow Leis & Carson-Ewart (2004). Lengths are Standard Length (SL). Percentages are of SL. Illustrations in Fig. 1 were prepared with the aid of a camera lucida, and Fig. 2 was made with a Leica digital photomicrograph system. Pigment refers to melanophores in preserved specimens. Specimens examined are deposited in the Australian Museum, Sydney (AMS), Institute of Oceanic Research and Development, Tokai University (IORD), and the National Science Museum, Tokyo (NSMT).

Identification. The larvae were identified as lutjanids through the characteristics listed by Leis & Rennis (2004): including 24 myomeres; laterally compressed body and head; very long dorsal-fin spines (particularly the second) and pelvic-fin spines; fin spines that are very weakly serrate to smooth; longest P_2 ray longer than P_2 spine; strong head

Table 1. Meristic characters of *Macolor* species, from Kishimoto *et al.* (1987).

species	dorsal fin	anal fin	pectoral fin	gill rakers	lateral-line scales
Macolor macularis	X, 13–14[a]	III,10	17	109–122	50–53
Macolor niger	IX[c]–X,13,14,15[c]	III,10[b]–11	16[b],17,18[b]	89–108	49–58

[a] in <20% of individuals, [b] in <10% of individuals, [c] in <5% of individuals.

spination without serrations on preopercular spines; head spination includes weak anterior frontal ridge, supraorbital ridge, weak pterotic ridge, and spines on opercle, subopercle (in larger individuals) and interopercle, and on inner and outer borders of preopercle; spines also present on bones of the pectoral girdle, including posttemporal, supracleithrum, and dorsal postcleithrum; no supraoccipital crest or spines; no lachrymal spines or serrations.

The larvae were linked as a series through their meristic values and their pigment pattern, most particularly the pigment on the opercle and urostyle. They were identified as belonging to the genus *Macolor* through their fin-ray counts of DX,14–15, AIII, 10–11, P_1 17–18, and high number of gill rakers (c. 55 rakers in settlement-stage larvae of *M. niger*, and c. 70–74 and c. 47–65 in the settled individuals identified as *M. niger* and *M. macularis*, respectively). Among lutjanids, only *Macolor* spp have this combination of meristic values. No Indo-Pacific lutjanines other than *Macolor* spp have more than 30 gill rakers, whereas *Macolor* spp have at least 89 rakers as adults (Allen & Talbot, 1985; Allen, 1985; Kishimoto *et al.*, 1987). Some species of the caesionine lutjanid genera *Caesio* and *Pterocaesio* have fin-ray counts within the range of the larvae described here, but they have fewer gill rakers (<40 as adults: Carpenter, 1987). In any case, their larvae have been described and can be distinguished by other characters, most especially by their strongly serrate fin spines and more slender body (Reader & Leis, 1996).

The larvae were identified as *Macolor niger* by their fin-ray counts of DX,14–15 (*M. macularis* has DX,13–14), and AIII,10–11 (one of eight with 10 rays—*M. niger* rarely has 10 anal-fin rays, whereas *M. macularis* is not known to have 11, Table 1). Further, the pigment pattern of the settlement-stage larvae matches that of recently settled *M. niger* as described by Kishimoto *et al.* (1987).

Three recently settled *M. macularis* had fin-ray counts of DX,13 and AIII,10, confirming their identification. Further, their morphology and pigment pattern match that described for the species by Kishimoto *et al.* (1987).

Descriptions

Macolor niger (Forsskål)

Table 2, Figs 1, 2

Two pelagic larvae, 4.8 & 10.0 mm: NSMT-PL 149 (West Pacific: 7°56'S 161°04'E), NSMT-PL-188 (West Pacific: 3°15.2'S 151°05'E). 4 settlement-stage larvae, 16.1–19.3 mm: AMS I.43883-001, -002, -003 (Great Barrier Reef), AMS I.43869-001 (Nusa Nane Isl, Solomon Isls). 2 recent recruits, 26 & 32 mm: AMS I.34722–001 (Upolu Isl, Samoa), IORD 83–275 (Iriomote Isl, Ryukyu Isls).

Body compressed and deep, but decreasing in depth from 50% at 4.8 mm to c. 37% at settlement. Body deeper at P_1 base than at anus, but this differential decreases with growth (Table 2). Gut coiled and compact, with virtually no gap between anus and anal fin. Prominent gas bladder immediately dorsal to gut. Caudal peduncle of moderate depth and length. Myomeres 24 (10–11+13–14). Gill rakers c. 55 at settlement, c. 70 at 26 mm and c. 75 at 32 mm.

Head bluntly triangular, compressed and large, decreasing in relative size from c. 45% at 4.8 mm to 35–38% at settlement. Snout less than eye diameter and bluntly triangular, becoming rounder following settlement. Mouth large and moderately oblique; tip of maxilla reaching to a

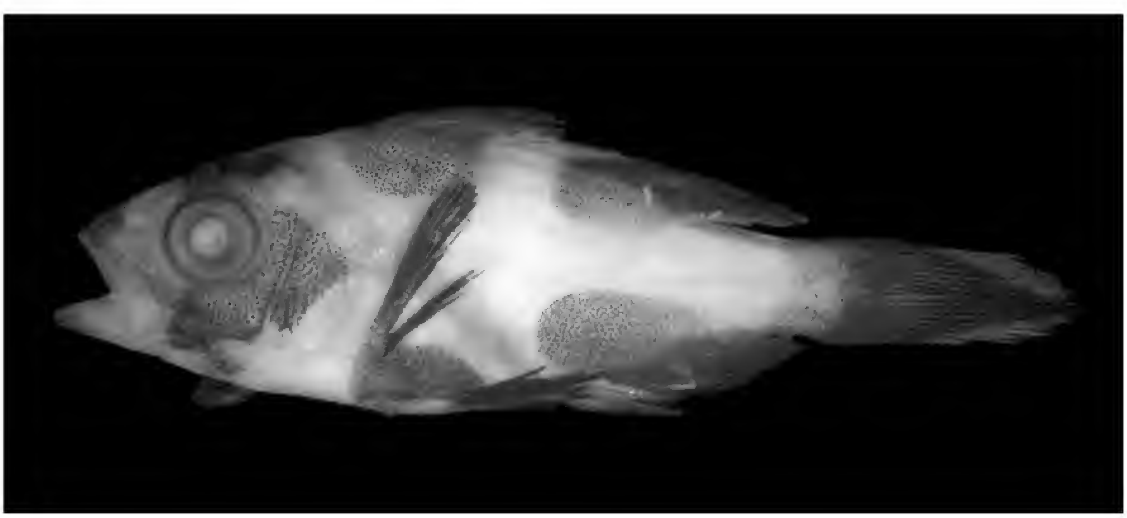

Fig. 2. Settlement-stage larva of Macolor niger from the Great Barrier Reef (19.3 mm, AMS I.43883–003). Note that pectoral fin (heavily pigmented) is folded upward. Photo by M. Lockett.

Table 2. Morphometric (in mm) and meristic values for *Macolor* larvae and recently-settled individuals. Abbreviations are: PreAL, preanal length; PreDL, predosal-fin length; HL, head length; ED, eye diameter; SnL, snout length; BD (P_1), body depth at P_1 base; BD (anus), body depth at anus; PedL, caudal peduncle length; D, A and P_1 refer to dorsal, anal and pectoral fins; sp is spine; PreopAng sp, preopercle angle spine. *d*, damaged; *i*, incipient rays.

	SL	PreAL	PreDL	HL	ED	SnL	BD (P_1)	BD (anus)	PedL	Dsp1	Dsp 2	Dsp 3	P_2 sp	P_2 ray 1	Preop Ang sp	D	A	P_1
Macolor niger pelagic																		
NSMT PL149	4.8	3.0	2.0	2.2	0.8	0.6	2.4	1.7	1.2	0.5	1.7	1.0	1.2	1.5	0.8	IX(I),15	III,11	10+*i*
NSMT PL-188	10.0	6.0	3.8	4.3	1.5	1.1	4.7	3.8	1.7	1.0	3.3	2.7	3.1	3.1	1.1	X,14	III,11	18
Macolor niger settlement-stage																		
AMS I.43883–002	16.1	8.9	5.8	5.7	2.1	1.6	6.2	5.2	3.7	1.8	4.8	4.2	3.9	4.8	1.4	X,14	III,10	17
AMS I.43869–001	17.4	9.9	6.6	6	2.4	1.5	6.3	5.5	3.8	1.2	3.3	3.5	3.9	4.5	1.3	X,14	III,11	18
AMS I.43883–001	17.6	10.2	6.4	5.9	2.1	1.9	6.6	*d*	3.3	1.2	4.1	4.1	3.8	4.8	1.2	X,14	III,11	17
AMS I.43883–003	19.3	11.2	7.0	7.4	2.7	2.2	7.2	6.3	3.9	1.3	3.7	4.0	4.0	5.5	1.2	X,14	III,11	18
Macolor niger settled																		
AMS I.34722–001	26.0	16.9	9.7	10.7	3.4	2.7	9.4	8.6	5.3	*d*	4.5	*d*	4.9	7.8	1.0	X,14	III,11	18
IORD 83–275	32.3	18.2	11.2	11.5	4.5	2.2	11.1	10.1	7.1	*d*	*d*	*d*	5.5	10.4	0.5	X,14	III,11	17
Macolor macularis settled																		
IORD 82–299B	16.8	9.8	5.9	6.6	2.3	1.5	7.2	6.1	3.5	*d*	*d*	*d*	5.1	10.8	0.8	X,13	III,10	17
IORD 85-316	17.3	9.5	6.5	7.1	2.5	1.6	6.4	5.6	4.2	1.8	6.6	5.2	5.7	10.3	0.9	X,13	III,10	17
IORD 82–299A	20.3	12.4	7.5	8.2	3.1	1.9	8.7	7.4	4.6	1.4	d	4.7	6.5	13.5	0.8	X,13	III,10	18

level between anterior edge of eye and pupil. Canine teeth present in all specimens. Nasal pit unroofed at 4.8 mm, but two nostrils present by 10 mm. Scales start forming over most of the body at about 17 mm, and by 19 mm a full set of scales is present.

Spination on head well developed, and spines smooth. The longest head spine, a strong spine at angle of preopercle, decreases in relative length from 16% at 4.8 mm to c. 6% at settlement, and rapidly after settlement to c. 2% at 32 mm. On outer border of preopercle, two moderate size spines are located immediately adjacent to angle spine, one above and one anterior. Other spines on preopercle outer border are small. On outer, upper limb, there is no small spine at 4.8 mm, but one appears by 10 mm, and settlement-stage larvae have 10–13 small serrations that decrease to c. 8 in the 26 mm recruit. On the lower outer limb, there are 2 small spines at 4.8 mm, increasing to 4 by 10 mm, and 5–6 by settlement: in recruits, the lower, outer limb extensively and finely serrated. Spination on the inner preopercular border smaller and more limited. Lower, inner border with 3 small spines at 4.8 mm, 5 by 10 mm, and 6 by 16 mm, but these become eroded and ultimately lost by 19 mm. Inner, upper border with a single, small spine by 10 mm that is lost by 19 mm. Opercle has a single spine. Subopercle lacks spines until 18 mm, when a single, small spine is present, increasing to 3 small spines at 19 mm: these do not increase in number or size following settlement. Interopercle with a single spine just dorsal to the preopercular angle spine until settlement, when the ventral edge also becomes serrate. The supraorbital ridge smooth at 4.8 mm, with 5–6 weak spines posteriorly by 10 mm. These reduced to 3 eroded spines by 17 mm and absent in the settled individuals.

A small spine present on dorsal postcleithrum in 10 mm and larger individuals (absent in 4.8 mm larva). Two large supracleithral spines present at 4.8 mm, three in 10–17.6 mm larvae, two in the 19.3 mm settlement-stage larva, and only a single, tiny spine in settled individuals. A single dorsal posttemporal spine present in 4.8 and 10 mm larvae, one or two dorsal spines in 16–17 mm settlement-stage larvae, three at 19 mm, and 6–9 in the settled individuals. A single ventral posttemporal spine is present from 10–19 mm, but the settled individuals have 2–4 spines. A pterotic ridge is present by 10 mm, and a frontal ridge by 16 mm.

In 4.8 mm flexion-stage larva, a full compliment of 9+8 primary caudal rays present. Based on other lutjanids, flexion probably complete before 6 mm. All elements of D, A and P_2 fins present in the 4.8 mm larva, with last spine of D fin transforming from a soft ray to a spine. P_1 fin of 4.8 mm larva has 11 rays plus incipient rays, but the 10 mm and larger individuals have a full compliment of P_1 rays. Fin spines robust and chevron-shaped in cross-section, except P_2 spine which has two leading-edge ridges, and is concavely trapezoidal in cross-section in all specimens. Weak serrations present on the trailing edges of many fin spines. In 4.8 mm larva this includes D spines 1–6, A spines 1–2, and P_2 spine. At 10 mm, trailing edge serrations are present only on D spines 2–4, A spines 1–2 and P_2 spine. A portion of leading edges of fin spines have very weak serrations at 4.8 mm (Dsp 2, P_2) and 10 mm (Dsp 2–3, P_2, Asp 1–2). Fin spines smooth or nearly so in settlement-stage larvae: 16 mm larva has a few inconspicuous, eroded serrations on the trailing edges of Dsp 1 and Asp 1, and barely visible eroded serrations on the leading edge ridges of P_2 sp. At 4.8 and 10 mm, there is no obvious internal structure in fin spines, but settlement-stage and settled individuals have fine reticulate internal structure in larger fin spines. Dsp 2 is longest fin spine in the two pelagic larvae (32–35% SL), but by settlement, Dsp 2, Dsp3, and P_2sp are of similar length (c. 20–24%SL). A spines become more robust than D spines from about 10 mm. First ray of P_2 fin longer than spine, a disparity that increases with development especially following settlement.

Pigment: Larvae are lightly pigmented, but pigment intensifies as settlement approaches. The 4.8 mm larva has a single, small ventral melanophore on the caudal peduncle. The 10 mm larva has no ventral pigment, but the peduncle melanophore may have moved to an internal position just ventral to the urostyle. Both 4.8 and 10 mm larvae have a single, intense, internal melanophore in a saddle-like position on urostyle. Both melanophores near the urostyle persist in settlement-stage larvae, although they become increasingly difficult to see as external, lateral pigment intensifies (see below). No ventral pigment forms on the abdomen or head until settlement approaches. Similarly, no dorsal pigment forms on tail or trunk until settlement. At 4.8 mm, there is a single dorsal melanophore on the midbrain, but by 10 mm, both mid- and forebrain are largely covered dorsally and laterally by dense, evenly-spaced melanophores: these are retained. The 10 mm larva has internal melanophores on hindbrain both dorsally and ventrally. At the base of opercular spine, the 4.8 mm larva has a prominent melanophore, and the 10 mm larva has a cluster of large, prominent melanophores, which are retained in settlement-stage larvae. The gas bladder and dorsal surface of the gut are covered by a saddle of melanophores. The fins of the 4.8 mm larva lack pigment except for a single, distal melanophore in the trailing-edge chevron groove of Dsp2, and two melanophores, one each at base of two caudal rays. By 10 mm, the spinous dorsal fin is extensively pigmented, with the distal portions of fin membrane and spine chevron groove covered with fine melanophores. The area covered decreases from about two thirds anteriorly to only a few distal melanophores posteriorly (Fig. 1B). In addition, a few melanophores are present basally on membranes near soft rays 3–5. By 10 mm, P_2 fin has a few melanophores on soft rays 1 & 2 and membranes near the spine tip.

As settlement approaches, pigment intensifies and spreads, taking on aspects of the juvenile pigment pattern. The anterior half of the spiny dorsal fin becomes intensely pigmented, and this pigment spreads ventrally onto the lateral surface of the body, eventually forming a large black blotch extending nearly to the lateral line. Similarly, the middle portions of the soft dorsal fin become intensely pigmented, and this pigment spreads ventrally to form a second, large blotch extending to the lateral line. Following settlement, these two blotches merge along the back, leaving unpigmented the middle portion of the dorsal fin. The pigment extends along the dorsal surface of the caudal peduncle to join the caudal pigment. The posterior third of the caudal peduncle becomes heavily pigmented, as does the caudal-fin with the exception of the distal portions of the dorsal-most and ventral-most rays. Pigment also extends along the ventral surface of the caudal peduncle, joining a large blotch extending dorsally from the heavily pigmented soft rays of the anal fin. The pelvic fin becomes heavily pigmented, and this pigment then extends dorsally to the base of the pectoral fin before settlement. The pectoral fin also becomes heavily pigmented. The heavy brain and opercular pigment present at 10 mm spreads and coalesces and then spreads across the cheek below the eye to form a large blotch extending as far forward as the anterior edge of the eye by settlement. Finally, a separate small cluster of pigment forms at the tip of the snout. In life, the portions of the body that are not black are coloured white, resulting in a striking, and distinctive pattern (in contrast, non-black portions of the fins remain unpigmented). The distinctive post-settlement colour pattern is illustrated by Kishimoto *et al.* (1987) and Randall (2005).

Remarks. Larvae of *M. niger* smaller than 4.8 mm are likely to have more extensive fine serrations on the fin spines, and also more pigment ventrally on the tail, if patterns of development are similar to those of other lutjanine species (Kojima, 1988; Watson & Brogan, 1996; Leis & Rennis, 2004; Lindeman *et al.*, 2005; JM Leis, unpublished). The very limited pigment on the head and fins of the 4.8 mm larva is unusual for a lutjanine species. The distinctive saddle-like melanophore on the urostyle may be present in smaller larvae. The fine serrations of the fin spines if present in smaller larvae, combined with the pigment characters above may assist in the identification of smaller larvae, as will the distinctive fin-ray counts.

Larvae of *M. niger* have all diagnostic characters of lutjanids, thus confirming the placement of *Macolor* as a lutjanid genus. Without access to larvae of *M. macularis*, no larva-based test of *Macolor* monophyly can be made, but there is nothing particularly distinctive about the development of *M. niger* that would support *Macolor* monophyly, considering the range of larval morphology and development evident in other lutjanine genera. In contrast, the fact that both *Macolor* species share similar and otherwise unique ontogenetic changes in colour and body shape following settlement seems to indicate that the two species do form a monophyletic group.

The general morphology of *M. niger* larvae is similar to other lutjanines, but the monophyly of the Lutjaninae remains to be established. Larvae of basal lutjanids (i.e., species in the subfamilies Etelinae and Apsilinae, sensu Johnson, 1980) lack two apparently derived characters present in the other three lutjanid subfamilies (i.e., Paradicichthyinae, Lutjaninae, and also Caesioninae, sensu Johnson [1980], which is clearly a lutjanid subfamily; see also Reader & Leis [1996]). These characters are a second ridge on the leading edge of the P_2 spine and delayed formation of the second and subsequent spines on the outer, upper edge of the preopercle (Leis, 2005). Lutjanines and caesionines have serrations on the supraorbital ridge that is lacking in the other subfamilies, although one of the two paradicichthyine species also has serrations on the supraorbital ridge (Leis & Bray, 1995). These three characters are present in *Macolor niger* larvae, and the second P_2 ridge is present in newly settled juveniles of *M. macularis* (supraorbital serrations are absent, as would be expected following settlement, and it is not possible to determine the sequence of formation of the preopercular spines from settled juveniles alone). This corroborates the placement of *Macolor* with the lutjanines and caesionines, but, as yet no characters of larvae support monophyly of the Lutjaninae.

Macolor macularis Fowler

Table 2

Three recently settled individuals, 16.8–20.3 mm: IORD 82–299A, 82–299B, 85–316, Iriomote Isl, Ryukyu Isls.

Body deep (37–43% at P_1 base: 32–36% at anus), with large head (39–40%): body fully scaled. There are c. 47–65 gill rakers, increasing in number with size.

The longest head spine, a strong spine at the angle of the preopercle, is c. 4–5%. On outer preopercle border, two moderate-size spines located immediately adjacent to the angle spine, one above and one anterior to it. Other spines on the preopercle outer border are small: 12–17 serrations on upper limb, and 4–7 serrations on lower limb. No spination remains on inner preopercle border. Opercle has a single spine. The 16.8 mm specimen has a single, small spine on each of the subopercle and interopercle, whereas the larger specimens lack spination on either bone. The supraorbital ridge is overgrown and no longer visible. A small spine present on dorsal postcleithrum. A single supracleithral spine and 3–5 posttemporal spines present.

Fin spines smooth and robust, with some internal structure. Both Dsp 2 and 3 long (38% and 23–30%, respectively). P_2sp long (30–33%) and P_2 ray 1 very long (60–67%).

Remarks. At settlement, *M. macularis* seems to be a few mm smaller than *M. niger*, with a slightly deeper body and much longer elements in the spiny dorsal and pelvic fins. Head spination is similar in the two species, as is general morphology with the exceptions noted above. Pigment in recently settled *M. macularis* is similar to that of *M. niger*, but differs in detail (Kishimoto *et al.*, 1987).

Based on comparison of recently settled individuals, it is reasonable to expect that pelagic larvae of *M. macularis* will be similar to those of *M. niger*, but possibly somewhat deeper-bodied, and with longer elements in the spiny dorsal and pelvic fins. Probably, *M. macularis* larvae have weak serrations on fin spines similar to those of *M. niger*.

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